Understanding Piping Plover Population Dynamics through Mathematical Model, with Application to Northern Assateague Island, Maryland, and Long Island, New York, Barrier Beaches

By

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ABSTRACT

The piping plover (*Charadrius melodus*) is a small migratory shorebird that breeds in three geographic areas: along the Atlantic Ocean coast; sandy beaches of the Great Lakes; and along major rivers, lakes, and wetlands of the northern Great Plains of the United States. This federally listed endangered species is dependent upon non-vegetated to sparsely vegetated sandy areas near bay, lake, and ocean intertidal areas for breeding, and it has experienced population declines due to reduction in habitat along developed and stabilized coasts, increased predation, and human disturbance. This paper explores a simple mathematical model, the logistic equation, which appears to represent leading factors governing a plover population. The model was found to describe plover population data from two locations on the Atlantic coast: northern Assateague Island, Maryland, and the south shore of Long Island, New York. Model predictions and possible applications are discussed in the context of a potential aid for plover management.

ADDITIONAL KEYWORDs: Overwash, breaching, beach fill, coastal inlet, West Hampton Dunes

INTRODUCTION

The mathematical model described in this paper was stimulated by a presentation on piping plover (*Charadrius melodus*) breeding pair counts given by Jack Kumer, National Park Service, Assateague Island National Seashore (AINS), to a multi-agency collaborative committee providing oversight for the sand-bypassing project at the northern end of Assateague Island, Maryland. The AINS is the major breeding site for the piping plover in Maryland. Kumer was reporting on the 2004 piping plover breeding season with respect to a feature called the "storm berm" constructed as an emergency storm-protection action and ecosystem restoration project (Schupp 2005) by the U.S. Army Corps of Engineers (USACE) along the northern end of the island after opening of an ephemeral breach at that location during winter storms of 1998.

Since 2003, the USACE Baltimore District has had the objective of bypassing 138,000 cu m (180,000 cu yd) annually to the nearshore of northern Assateague Island (Figure 1) to restore the beach by dredging sand from the ebb shoal and flood shoal of Ocean City Inlet, Maryland, supplemented by offshore borrow sources. This inlet is located updrift of Assateague Island. The 5.2-km (3.2-mile) -long storm berm appears to have prevented overwash that was anticipated to occur during subsequent years. The fresh sand comprising overwash fans provides favorable breeding and nesting habitat for the piping plover. At present, the storm berm serves as a major nesting area for the piping plover in the AINS, but it is not considered of high quality because of distance to the bay perimeter for foraging. As a consequence, in January 2005 staff of the AINS, Baltimore District, other agencies, and local government agencies collaborated in implementing a plan for notching the storm berm to create areas with improved overwash potential (Schupp 2005). A newly developed regional breaching model (Kraus and Hayashi 2005) was run to develop and explore designs.

The AINS annually tracks piping plover numbers on Assateague Island. The USACE New York District, through contract with Virginia Tech at Blacksburg, Virginia, has similarly been tracking plover populations for the barrier beaches on the south shore of Long Island, New York. Locations of these areas are shown in Figure 1, which depicts the breeding range of the piping plover on the U.S. Atlantic coast. One of the earliest and most comprehensive observations of piping plover behaviors and population dynamics was conducted on the barrier beaches of eastern Long Island, New York, (Wilcox 1959) extending from Moriches Inlet to Shinnecock Inlet and later including Mecox Bay, covering the area now known as West Hampton Dunes (Figure 2). The qualitative and quantitative observations at the AINS and on eastern Long Island provide valuable information and data for mathematical modeling of piping plover populations.

Population size for piping plovers depends on numerous factors. A leading factor is the amount of available breeding and nesting habitat (hereafter, usually referred to as "habitat"), which is related to beach management on developed coasts. With the objective of understanding population dynamics of piping plovers, a simple

Figure 1. Breeding range of Atlantic Coast Piping Plover (adapted from NYDEC Web site).

Figure 2. Location map for Long Island, New York, barrier islands, inlets, and bays.

mathematical model is explored that appears to have some utility in interpreting numbers of breeding pairs counted and thereby in aiding management approaches for creating and preserving piping plover habitat.

PIPING PLOVERS

In 1986, the piping plover, a migratory shorebird, was listed as a federal threatened species under the Endangered Species Act of 1973. In North America, the piping plover breeds in three geographic regions: the Atlantic coast (portions of which are discussed here), the Great Lakes, and the Northern Great Plains. The Atlantic coast population breeds on sandy beaches from Newfoundland to North Carolina (Figure 1), arriving to breeding grounds in early spring. Preliminary counts for 2004 found only about 1,650 breeding pairs on the Atlantic coast (http://www.fws.gov/northeast/pipingplover/status/preliminary.04.pdf). Nests are placed above high tide on open beach sand with minimal vegetation (Haig and Elliott-Smith 2004). Quoting Wilcox (1959), "…Piping plovers on Long Island (New York) favor dry sandy outer beaches."

During May and June, one egg is laid every other day until an average clutch of slightly less than four eggs is complete. The young leave the nest shortly after hatching and fledge after about 25 days. Plover diet consists of marine worms, insect larvae, beetles, crustaceans, mollusks, and other small marine animals, obtained by foraging at bay, ocean, and ephemeral pond intersections with land. Adult plovers and plover chicks are vulnerable to predators hiding in vegetation, and the chicks cannot walk through dense vegetation between the nest and waterside foraging areas. Open sand or sand pathways between nesting areas and foraging areas is necessary (Haig and Elliott-Smith 2004). Wilcox (1959) found that many adult plovers return to the same nesting area annually if the habitat remains suitable, and they may tend to retain the same mate as well. By August and early September, most plovers have begun migrating south to wintering areas (Haig and Elliott-Smith 2004). Piping plovers spend winters along the coast from Texas to North Carolina and, infrequently, as far south as the Bahamas and Greater Antilles.

Plovers breed on dry sandy beaches composed of fresh or recently accreted sand such as found near the ocean and bay shores of barrier islands; on overwash fans, near newly cut or evolving breaches and inlets; or on dredged material placed on shore for beach nourishment. Plovers are most successful if such breeding areas are located near bay, ocean, or pond water peripheries, where food sources are most abundant. There is evidence that bay intertidal shore and ephemeral pools promote greater foraging success than the ocean shore (Patterson et al. [1991] and Loegering and Fraser [1995] for Assateague Island; Elias et al. [2000[] for Long Island, New York, barrier islands). Elias et al. (2000) found that bay shores and ephemeral pools had larger numbers of arthropod abundances than the energetic swash zone of the ocean on the Long Island south shore. Plover chicks will travel on vegetation-free paths between their nests and the ocean, bay, or pools to forage, if such paths are available. If the paths are long and competition is keen, chicks are endangered by aggressive behavior of both breeding and non-breeding plover adults in attempting to reach food sources.

There is a large literature on population dynamics of birds (e.g., Newton [1998] and references therein). Piping plovers are classified as endangered by the state of New York, and the New York State Department of Environmental Conservation (NYDEC) provides an informative summary of the life history, distribution, habitat, and research needs for Atlantic coast piping plover (http://www.dec.state.ny.us/website/dfwmr/wildlife/endspec/piplfs.html/). The U.S. Fish and Wildlife Service has developed a Piping Plover Atlantic Coast Recovery Plan that provides a wealth of synthesized information and numerous references (http://www.fws.gov/northeast/pipingplover/index.html). The Cornell Laboratory of Ornithology published a comprehensive document on the life history of piping plovers, considered an authoritative source for this type of information on the species (Haig and Elliott-Smith 2004). These references can be consulted for further information about piping plovers.

POPULATION DYNAMICS MODEL

Numerous factors control or modify the population size of migratory birds. Extreme events or unfavorable conditions in wintering areas, such as major storms, may reduce numbers returning to breeding grounds without any apparent cause and effect for an observer monitoring birds at the breeding location, for example. As described in the preceding section, factors known to control productivity include availability of habitat, availability of food and means to reach the food, predation, disturbances such as from human activity, and fecundity of the breeding pairs – which is related to the preceding and other factors. Birds may also move from one breeding location to another, and immigration and emigration may need to be considered in detailed accounting of plover populations.

Another and central governing factor controlling population is the aggressive conspecific behavior of plovers. For example, Kumer (2005) found in his 2004 observations on the AINS that non-breeding plovers occupied some of the most valuable foraging habitat, displacing breeding plovers and their chicks to secondary habitats. Competition among plovers in high-density populations appears to be a significant contribution to population reduction. These factors are noted to put the simple model introduced below in perspec-

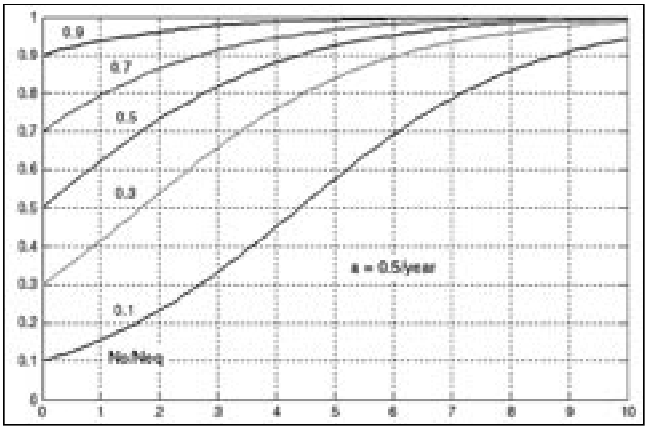

Figure 3. Dependence of modeled population as function of initial number of pairs.

tive of complex species behavior and environmental conditions at multiple locations.

Derivation of Model

The model for governing the population size of piping plovers in a given area accounts for their reproductive potential and their competitive interactions. It is a standard model that appears to describe the leading controls on breeding pairs for a wide range of species (Edelstein-Keshet 1988). The model was formulated to describe the number of plover pairs rather than individuals, because such information is typically reported, and the number of breeding pairs will increase the population, not the total number of individuals. The total plover population will contain a significant, but smaller number of nonbreeding birds. Let $N(t)$ be the number of breeding plover pairs at a given time, t. Then the governing equation for the rate of change of breeding pairs N is:

$$\frac{dN}{dt} = aN - bN^2 \qquad (1)$$

The first term on the right side states that the increase in number of breeding plover pairs depends on the number of pairs that is present, with a representing a breeding efficiency or growth coefficient. The coefficient a contains contributions from numerous factors, possibly expressible as $a = a_1 + a_2 - a_3 + a_4 - a_5 + \ldots$, where a_1 and a_2 represent growth contributions associated with quantity and quality of habitat, respectively; a_3 a reduction in growth by predation (with $a_3 = 0$ denoting no predation); a_4 an increase by immigration,;a_5 a decrease in growth by emigration; and so on. The analysis in this paper does not isolate the possible individual contributions, and it is doubtful that a data set exists to do so at this time.

The second term on the right side, having a negative sign, represents the mutual interaction between individual plovers. It can be interpreted as a plover-to-plover competitive interaction, hence is multiplicative as the square of N. It can also be understood as representing the surface area occupied by the breeding pairs present, which gives a square of the number of breeding pairs, because each pair requires a certain average area for breeding and nesting. Although Eq. 1 is nonlinear, it is solvable in closed form if the coefficients are constants.

The initial population size N_0 must be known to start operation of the model. The initial number of plover breeding pairs must be at least equal to 1, so that population growth is possible by the first term on the right side. For small numbers of individuals, the second term as the square of N is small. However, as the population (N) grows, the interaction term becomes large because more birds must compete for limited habitat area.

The coefficient b represents complicated plover-plover interactions limiting the population. It can be eliminated if knowledge exists of the equilibrium number of plovers that can be present at a given location within a known habitat area. Plovers compete fiercely for food and breeding territory, and a particular suitable habitat can only support a long-term average maximum number of individuals. The equilibrium population size is not the same at all locations because of various factors such as distance to and quality of food sources, presence of predators, and disturbances. The population in equilibrium is denoted as N_{eq}, found by setting the left side to zero in Eq. 1 (representing equilibrium, which means no rate of change in population size). Then the growth term on the right side of Eq. 1 equals the mutual interaction term, yielding:

$$b = \frac{a}{N_{eq}} \qquad (2)$$

Thus, b can be expressed in terms of quantities obtainable through general observation and analysis. If the interaction coefficient b is considered an intrinsic property of a particular species and independent of environmental factors, its value should be approximately constant for that species. Under this assumption, Eq. 2 states that there is a proportionate relation between a and N_{eq}, expected to hold for a specific plover population.

If the coefficient a is constant, and environmental conditions at the breeding and nesting habitat remain constant so that N_{eq} is constant, the solution of Eq. 1 is found to be:

$$N = \frac{N_{eq}}{1 + \left(\frac{N_{eq} - N_0}{N_0} \right) e^{-at}} \qquad (3)$$

To calculate values of N through time by Eq. 3, three quantities must be known: the initial population, N_0; the equilibrium population, N_{eq}; and the growth coefficient a, which has the dimensions of 1/time. Sustained observations of plovers and habitat over several years can provide data to estimate these quantities. Constancy of a and N_{eq} implies no change in conditions that influence plover populations, and such an assumption cannot be expected to hold over more than several years, either in the natural environment uninfluenced by society or on developed beaches without careful management. For example, vegetation will gradually appear on newly formed overwash fans.

To examine the properties of Eq. 3, a sensitivity analysis was performed by calculating the population as a function of time for a = 0.5/year (order of magnitude as found below in comparison to data) and various initial population sizes N_0 from 10 percent to 90 percent of the equilibrium population. The results are shown in Figure 3, where the number of plover pairs is expressed as a fraction of the equilibrium number, N_{eq}. For the situation of low initial numbers, growth is rapid for the first several years, and then the increase in the rate decreases as the competition term becomes stronger. For larger initial population sizes, growth to equilibrium number occurs sooner than for low initial numbers, but the rate (slope of curve) is less because the competition term is large compared to the growth term in Eq. 1. For this value of the growth coefficient, which is similar to values found below in fitting the model to field observations, equilibrium is attained or approached after about 5-10 years.

Equilibrium Population Density, Long Island

The equilibrium population size of breeding pairs, N_{eq}, is a key parameter entering the model and is the long-term average maximum number of sustainable breeding pairs for the given surface area of nesting and foraging habitat. "Long-term average maximum" refers to the average of the fluctuating record of annual maximum pairs observed over several years. An equilibrium population density describes the long-term average maximum number of breeding pairs per unit surface area. Such data were readily available to this study in publications pertaining to the south shore of Long Island.

Wilcox (1959) banded and observed piping plover almost continuously between 1937 and 1958 (as well as intermittently before that time), the beginning part of this period representing an era when the area between Moriches Inlet and Shinnecock Inlet, Long Island, was sparsely populated and in a near-pristine state. The era included overwash and new shoreline fringes that provided excellent plover habitat created during the September 1931 hurricane that breached the barrier and opened Moriches Inlet, and during the 1938 "Great New England Hurricane" that opened Shinnecock Inlet and caused massive overwash and breaching along the Long Island south shore barriers (Brooks 1939; U.S Army Engineer District, New York 1939).

Wilcox (1959) stated: "…seldom will one pair nest nearer than 100 ft (30 m) from the nest of another pair. Nests found were usually spaced 200 ft (60 m) or more apart." If one assumes a square area of beach with 60 m on a side for each breeding pair, then one acre of habitat can support one breeding pair, and one hectare (2.47 acres) of suitable habitat can in principle support about 2.5 breeding pairs, which might reasonably be rounded to two breeding pairs given the observation of "...200 ft or more apart." Therefore, the data of Wilcox for a relatively pristine beach modified by overwash, and with time for foraging areas to develop, indicate a potential areal equilibrium population density of approximately two breeding pairs/hectare for prime habitat. Plovers tend to breed in lines along the beach strip of barrier shores, so the value of two breeding pairs/hectare is likely of correct order of magnitude, but an overestimate for beaches with partially vegetated backshores.

The beaches near the eastern inlets of the Long Island south shore have undergone considerable development, as well as stabilization against breaching through construction and maintenance of vegetated dunes. Development can bring additional predation by introduction of free-ranging pet cats and dogs, which have the potential to become feral animals. On the other hand, beach renourishment provides ocean-side habitat and foraging areas for plover. The author took the picture in Figure 4 on 28 July 2005, on the beach located directly east of Moriches Inlet (east jetty seen in the background). A portion of the closed-off plover habit area to the right in the picture was in the inter-tidal zone at high tide. Substantial portions of beach nourishment areas between Shinnecock Inlet and Moriches Inlet are reserved for plover habitat, as are sections of the bay perimeter. On the day of the picture, no piping plovers were observed along the beach from Shinnecock Inlet to Moriches Inlet, suggesting that these birds had already initiated migration toward wintering areas.

Data compiled from graphs appearing in Cohen et al. (2002, 2003) as shown in Figure 5 indicates that the present habitat condition found on Long Island cannot maintain two plover breeding pairs/hectare. These authors report counts for various locations along the south shore of Long Island, with each individual point plotted on Figure 5 representing a different location. A best-fit line through all the data points gives a slope of 0.91 breeding plover pairs/hectare. If the three points on the lower left of the plot are removed, the slope becomes 1.18 breeding plover pair/hectare. The recent report of Houghton et al. (2005), which is an extension and summary of other work including the aforementioned Virginia Tech reports of Cohen et al. (2002, 2003), found an equilibrium density of approximately one breeding pair/hectare of habitat for West Hampton Dunes, but that the density was declining. The equilibrium density at other locations on Long Island as studied by Houghton et al. (2005) was closer to 0.5 breeding pair/hectare. As a summary rule of thumb, it can be concluded that present habitat supports at maximum approximately 0.5 to 1 breeding pair/hectare, identified as a modern-day condition equilibrium population density on the south shore of Long Island. Such information can be incorporated in the design of beaches and habitat, if piping plovers are potential part of the ecosystem.

Application of Population Model to AINS

Plover breeding pair counts for the AINS available from Kumer (2005) were plotted and compared to model predictions (Figure 6). The data set provides numbers of breeding pairs, but not of habitat area. In 1992 and again in 1998, the AINS experienced substantial overwash and near-breaching to create habitat well suited for piping plover. This habitat is expected to persist for several years before gradual colonization by vegetation.

The observed counts show a substantial increase from 1990. Therefore, the growth coefficient a was determined for different values of N_{eq} to minimize the square of the differences between calculated and observed breeding pair numbers from 1990 to 2005. A best fit was found for a = 0.45/year and N_{eq} = 62 pairs. Because the initial number of pairs in 1990 (14 pairs)

Figure 4. Designated piping plover habitat area to right of symbolic fencing, east of Moriches Inlet, 28 July 2005.

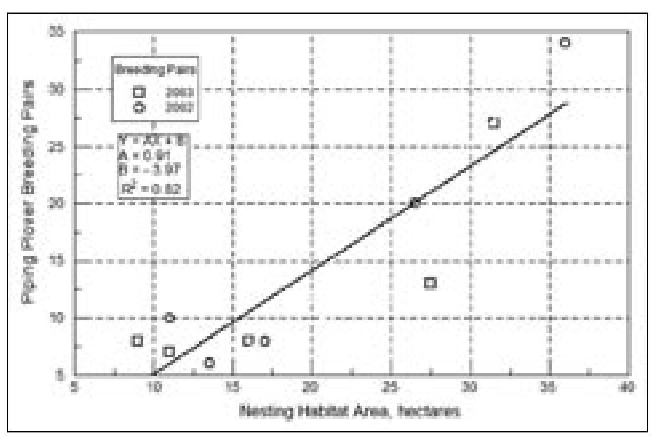

Figure 5. Dependence of piping plover breeding pairs on habitat availability, south shore of Long Island.

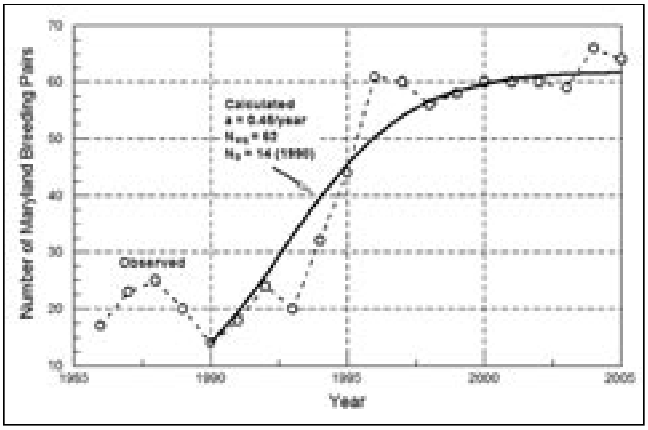

Figure 6. Number of known breeding pairs and model calculation, Assateague Island National Seashore, Maryland (observations from Kumer 2005 and Kumer – personal communication).

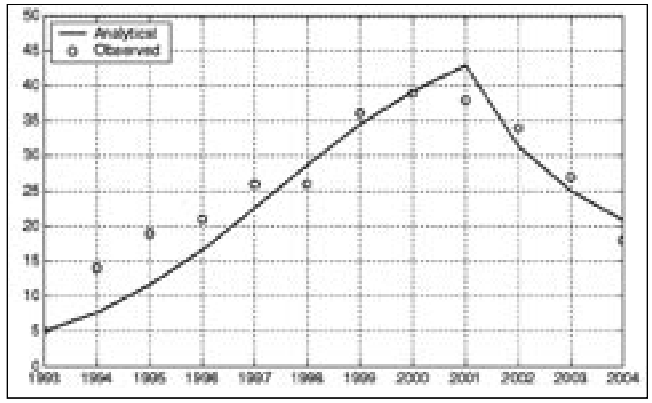

Figure 7. Number of known breeding pairs and model calculation, West Hampton Dunes, Long Island (observations from Houghton et al. 2005).

is relatively large as compared to the total maximum number observed (66 pairs), the calculated curve exhibits primarily exponential behavior (see Figure 3). The population model captures the trend in growth toward equilibrium. Referring to Eq. 2, the mutual interaction coefficient for this area is calculated as $b = 0.45/62 = 0.0073$/year/plover pair.

Application of Population Model to West Hampton Dunes

The village of West Hampton Dunes was incorporated in 1995 and is located between Westhampton to the east and Cupsogue County Park and Moriches Inlet to the west. The plover population in this area has experienced large vicissitudes by destructive and constructive forces on habitat as: (1) hurricanes in the 1930s-1950s that increased habitat by overwashes and breaches, (2) development along the ocean and bay sides of the barrier island that decreased habitat starting in the 1950s, (3) groin field construction along Westhampton in 1966 and 1970 that reduced downdrift beach width along what is now called West Hampton Dunes, and (4) breaching in the area in December 1992 and subsequent beach rebuilding and periodic nourishment commencing in 1996 (Bocamazo and Grosskopf 1999) that created plover habitat on the ocean side. The initial fill of approximately 1.9 M cu m (2.5 M cu yd) in the West Hampton Dunes was placed from July to October 1996; followed by the first renourishment from October 2000 to February 2001 of approximately 0.75M cu m (1 M cu yd). The initial nourishment and subsequent renourishment created a dune protected by a berm that advanced the narrow pre-1996 beach seaward 50 m (160 ft) or more, creating substantial potential piping plover habitat for about 3.2 km (2 miles).

Piping plover have been monitored in this area by staff of the Department of Fisheries and Wildlife Sciences, Virginia Tech, since 1993, first through sponsorship of the U.S. Fish and Wildlife Service, and in recent years through the USACE New York District. Houghton et al. (2005) compiled data, results, and conclusions of this 11-year effort, providing additional information about bird counts and habitat quantity and quality in West Hampton Dunes and in a reference area along the westernmost structures in the Westhampton groin field located to the east (Bocamazo and Grosskopf 1999).

The number of plover pairs counted along West Hampton Dunes is plotted in Figure 7. A clear trend of increase is seen from five pairs in 1993 to 39 and 38 pairs in years 2000 and 2001, respectively. After 2001, the number of pairs consistently and rapidly decreased. Houghton et al. (2005) investigated emigration as a main contributing cause of the decrease since 2001, as well as gradual vegetative encroachment over portions of the dunes placed as part of the beach nourishment. The Houghton et al. (2005) interpreted decline in population size by emigration rests on an assumed chick survival rate.

Another and likely dominant cause of the decline in breeding pairs since 2001, in the opinion of the author, concerns presence or absence of predator control, also discussed by Houghton et al. (2005). From 1996-2001, the Village of West Hampton Dunes voluntarily contracted with a trapper to take predators. Major predators are feral cats, foxes, and crows, although dogs and gulls will also attack plover adults and chicks. The village, which had been cooperating with piping plover conservation efforts (Daley et al. 2000), halted the contract after 2001 because of a dispute with the U.S. Fish and Wildlife Service over placement of symbolic fencing prior to the start of breeding season (Vegliante and Terchunian, in preparation). This fencing would have limited access of the beach to residents before the full breeding season considered by the village to commence once plover nests are observed.

In the population model, Eq. 1, an increase in predation or in any factor that would reduce reproductive success can be represented by decreasing the value of the growth coefficient a. However, if a changes (in this situation, decreases), the equilibrium number of pairs is expected to decrease because mutual interactions will be relatively more effective. In the present study, this relationship was specified by assuming the interaction coefficient b as given in Eq. 2 remains constant, which states that the ratio of the growth factor a to the equilibrium number of pairs N_{eq} remains constant.

The population model (Eq. 1) was applied by first fitting to the observations showing an increase (1993-2001), giving $a = 0.50$/year, and $N_{eq} = 50$ pairs. This value of N_{eq} is hypothetical or theoretical, because the population declined prior to achieving the potential equilibrium. Capability to estimate this potential equilibrium number is a strength of the mathematical model. The value of the mutual interaction coefficient for the increasing population time period at West Hampton Dunes then becomes $b = 0.50/50 = 0.01$/year/plover pair.

For the period of decrease in population size, 2001-2004, the population model was applied by taking N_0 to be the value calculated for year 2001 at the end of the increasing trend. By trial and error with constancy of b, a best visual fit was found for a = 0.05/year, giving N_{eq} = 5 breeding pairs. The model thus predicts a substantial decline in the plover population unless predator control is resumed and, possibly, unless breeding and foraging habitat is increased. The decrease in growth factor a as caused by the inferred increased predation is remarkable in being a factor of 10 and can be interpreted to mean that breeding success for this species is at a delicate balance of survival factors, for which a small perturbation can send the population plummeting (or, conversely, increase rapidly if the habitat becomes more favorable).

Inspection of the observations in Figure 7 indicates that the period 1993-1998 may have been a time when the population was approaching an equilibrium number for the given habitat and other conditions. If this interpretation is correct, a spurt in growth occurred in 1999 and 2000, perhaps related to improved management practice and wider beaches owing to nourishment. The different ranges imply different values of the growth coefficient a, and these periods could be modeled individually by the technique described in the preceding two paragraphs. However, one must be cautious with such data, in that moderate fluctuations in populations can be expected.

CONCLUDING DISCUSSION

The population dynamics of the piping plover was examined through operation of a mathematical model, the logistic equation, which accounts for growth and competition between individuals of the species. The model requires the initial number of breeding pairs, equilibrium number for a given area, and the value of a growth coefficient. For two different locations on the Atlantic coast, fitting to observations during times of sustained population expansion gave consistent values of model parameters as a growth coefficient a = 0.45-0.50/year and mutual interaction coefficient b = 0.0073-0.01/year/equilibrium number of pairs. Investigation of the equilibrium population density in this study and in review of others for the Atlantic plover population suggests a maximum upper limit of two breeding pairs/hectare for pristine habitat, with the present-condition habitat supporting 0.5 to 1 pair/hectare at dynamic equilibrium.

The population size model applied to West Hampton Dunes allowed estimation of the theoretical maximum (equilibrium) number of piping plover breeding pairs for the existing habitat, even though this limit was not reached, likely due to increased predation. The model was also shown to be capable of describing a decline in population by imposing a reduction in the growth coefficient and equilibrium number of breeding pairs, thus allowing a projection of the equilibrium number under the new, degraded environmental condition.

The mathematical model described here appears to hold value for compiling and interpreting data on piping plovers with focus on area of habitat, initial number of breeding pairs present, equilibrium density, and continuous record of annual counts. It was demonstrated that a full record need not be available for the modeling, with the flexibility available to reproduce population dynamics over distinct intervals of growth and decline in the total record length. Plover habitat management decisions may be aided by reference to model predictions to answer such questions as the growth rate to be expected at newly formed habitat, increase or decrease in growth rate in response to changes in habitat and predation, and the maximum number of breeding pairs to be expected for a given area. Knowledge of the equilibrium number of breeding pairs per unit area of habitat also aids in development of management goals. The population dynamics model could be linked to models of regional overwash and breaching as a wide-area management assessment and design tool, thus combining predictions of physical processes with those for the population of a threatened bird species. Sections of beach could thus be designed to provide habitat favorable to the success of piping plovers, with reasonable expectations on number of breeding pairs the habitat can support.

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